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THE SYSTEMATIC STUDY OF SOIL ECOSYSTEMS

(Chairman's Introduction)

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Traditional systems for the classification of soil are mainly based on geographical, vegetational or physical factors. Soil systematics based on the biology of soil organisms, although well established as a qualitative discipline, is now developing as a functional and quantitative science. Within broad limits set by geographical, geological and vegetational factors, certain main types of decomposition process occur and the quantities of materials and energy are measurable.

It is necessary now to make such measurements in relation to specific identifiable centres of activity within the soil. Newer techniques for localization and specific identification of organisms *in situ* promise early progress in this direction.

INTRODUCTION

There is a startling contrast between the systematic study of soils on the one hand and of soil ecosystems on the other. Biologists have been slow and hesitant to accept soil as a medium for ecological study and practising soil scientists have certainly done little to encourage their intrusion. This presumably stems partly from the considerable success of purely chemical approaches to soil science in the last century and partly from the daunting complexity of soil as a biological system.

The attitudes and conventions of physical sciences have certainly dominated much of the thinking not only of those interested in the physics and chemistry of soil but even of biologists who on a large scale have accepted the criteria of the pedologist and the soil chemist to an extent which, to a fresh-water biologist for example, would appear incredible. Many papers on soil fauna are still prefaced with details and descriptions of soil profiles according to the criteria of the pedologist, often extending to depths far beyond the habitat of the organisms under discussion, but usually in fact skipped by the reader because he knows from past experience that they will have little relevance to the biology of the soil. The reality is that soil ecosystems have a complexity of interrelations which render them largely independent of readily measureable physical, chemical and pedological characteristics. This results in the same or closely related species of organisms ranging beyond easily detectable boundaries defined by such considerations.

It appears to me that truly biological studies have penetrated soil science in two main fields. I hope to show that bringing biological knowledge to bear on these fields should do much towards uniting them. I refer to our increasing ability to associate known soil organisms with particular functions and secondly the understanding of functional processes of decomposition. Perhaps when these two approaches have been united we shall be able to offer to the soil scientist a real understanding and a truly systematic grouping of natural soils on a functional basis. This situation can only come about through a biological approach because, whether

SYSTEMATICS ASSOCIATION PUBLICATION No. 8, *The Soil Ecosystem*. Edited by J. G. Sheals, 1969, pp. 191–197.

he likes it or not, soils do contain organisms numbering millions to the square metre and it is the combined activities of these organisms which primarily determine the functional characteristics of soils.

POSSIBLE DETERMINANTS OF SOIL SYSTEMATICS

The characteristics of a soil and the organisms present are influenced by many external features. Four in particular have been used in the past as a basis for soil classification:

1. The nature of the physical material of which the soil is made up.
2. The geographical region in which it occurs, and consequently, the main climatic factors.
3. The vegetation growing on the soil.
4. The pedological characteristics of the soil itself: its structure and chemical and physical properties resulting from the first three factors, not only currently but also in the past.

It will be clear that these four factors are not independent but interact: extreme positions taken up in the past have exaggerated the role of each and neglected that of the others. This topic will not be reviewed here; the history of soil classification is discussed in many books including those of MOHR and VAN BAREN (1954), KUBIËNA (1953) and EYRE (1963).

Although none of these features alone is a complete determinant of community type, a relatively limited number of such external factors are of primary dominant importance in the systematic study of soil communities.

Geographical Factors

Broad geographical and climatic factors certainly set limits outside which certain kinds of soil community cannot occur. This formed the basis of the original Russian

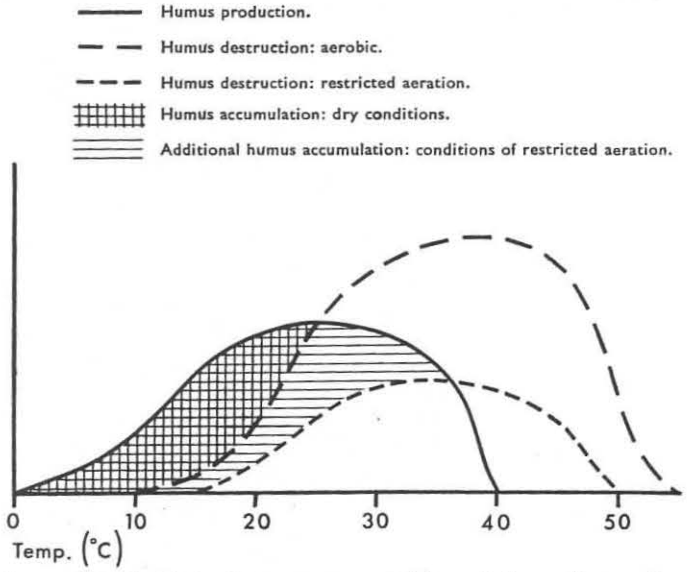

FIGURE 1. The combined effects of temperature and impeded aeration on litter accumulation (adapted from MOHR and VAN BAREN, 1954).

soil classification scheme which is also treated fully for instance by TISCHLER (1955). A single example at a more detailed level is that the influence of temperature and humidity on humus production and on humus destruction is not equal. This has been vividly illustrated by Mohr and van Baren in a diagram (*Figure 1*) which shows that, in general, humus accumulation can be expected to occur up to a mean annual temperature of about 25°C. When, however, the access of oxygen is restricted, as for example by excess rainfall, the destruction rate is lowered resulting in humus accumulation up to about 35°C. Under conditions of oxygen lack some anaerobes produce excess carbon which results in black soils, whilst the production of low pH conditions prevents bacterial growth and leads to the formation of peat.

It appears that these major different types of soil processes are associated with quite radically different faunal types, at least in the deeper layers. In some cases conditions occur in which certain groups cannot survive. The limited tolerance range of pH in certain earthworms (SATCHELL, 1955) and of most bacteria are examples. Of course when such major constituents of a community are lacking, fundamental changes in the remaining fauna and microflora occur, and there is a general belief that mull soils of higher pH are populated by proportionately more bacteria, nematodes and earthworms. More acid soils with a tendency to mor conditions contain more fungi, more mites and more Collembola (many of which tend to feed on fungi). Surprisingly few studies have been made on changes of fauna and microflora at soil and vegetation boundaries. I have unpublished notes showing almost complete changes in the small arthropods at a boundary between bracken-covered glacial-drift soil and a water-logged peaty soil in South Wales. But such information is of limited value because it relates to a 'chicken-and-egg' problem: a series of interrelated factors, soil, vegetation and aeration all change together. Clear information can only come from an experimental approach.

Vegetation

In one sense the vegetation is certainly of outstanding importance in determining soil communities. It contributes most of the litter and other organic matter which is the basis of the decomposer activities of the soil organisms. It is probable, too, that special attributes of certain litters can be major determinants of soil type and hence of the community. A clear example, for instance, is HANDLEY'S (1954) demonstration of the tanning properties of certain types of litter. These lead to the development of acid mor soils.

However, in another sense and on another scale, the vegetation can make surprisingly little difference to the soil community as regards the occurrence of particular decomposition processes, of particular groups of organisms and even of particular species. Within the range of my own experience for instance, I have collected the same or closely related species of small arthropods from arctic tundra and from a number of totally different British habitats. In addition the general facies of the micro-arthropod fauna has a very similar superficial appearance to that of many British woodlands in the Panamanian rain-forest soils which I have been examining recently. EVANS (1953) has reported British oribatid species such as *Damaeus onustus* from the East African mountains and WALLWORK (1958) and others have reported world-wide species from Michigan, from tropical West Africa and other areas.

On a small scale it is usual for changes in vegetation to bear little relation to changes in the fauna. I have found no significant association with species composition in two examples of vegetation micro-succession in a *Molinia* fen and more recently in *Calluna* heath in Jutland (Macfadyen and Brown, unpublished). There was however, some numerical variation in numbers of all the species on a common basis. In another study of rough tussocky grassland (mainly *Nardus* and *Molinia* in South Wales) all but a very few species were uniformly distributed regardless of the vegetation pattern.

A BIOLOGICAL BASIS FOR SOIL SYSTEMATICS

Spatial Zonation

One of the few broad generalizations that one can make about the soil-fauna is that the organisms living within a soil system at one time show a characteristic adherence to particular vertical zones. Within a family or order, for instance, some species generally live nearer the surface than others and this kind of habitat differentiation is so regular and so evidently of biological significance that typical 'life forms' have been successfully correlated with vertical habitat.

A classical example of such biological differentiation is provided by GISIN's (1943) study of Collembola. He recognized a series of forms ranging from deep-living, naked eyeless, unpigmented, springless genera such as *Onychiurus* and *Tullbergia*, through deep-litter species such as *Folsomia quadrioculata* which have short spines, reduced eyes, light pigmentation and a reduced springing organ or furca to species living on the soil surface, such as *Isotoma viridis*, with long spines, fully developed eyes, furca and pigmentation, and those living in vegetation which are in addition protected by scales and long spines. On a less dramatic scale there are many examples of genera, families and higher taxa which show marked specialization for particular depths and characteristic morphological adaptations.

For instance the Rhodacaridae amongst the Mesostigmata are small, lightly pigmented forms, well adapted for penetrating confined spaces in search of their prey. Most of the rest of the group, however, are surface-dwelling and possess converse features to these. Certain earthworms such as *Lumbricus rubellus* and *Allolobophora chlorotica* are deeply pigmented and live in litter rather than in soil: the white slender geophilids, symphylids and Pauropoda are the deep-living myriapods in contrast to most other chilopods and related groups.

But such vertically delimited soil faunas can be very widespread horizontally and can also vary quite independently of one another. This, to my knowledge, was first pointed out by STRENZKE (1949) who considered the existence of such independent groups within a major community to be outstanding examples of 'synusia' (characteristic faunas inhabiting what ELTON (1949) would call a microhabitat).

If it is true that we normally find a series of vertically independent patchworks of species groupings whose boundaries vary independently of one another and of the vegetation pattern, three important consequences follow: first, that in any attempt at systematic study of the soil faunas and if any sensible conclusions are to be derived from the study of the samples, the vertical boundaries must be detected and respected in sampling. Secondly the disposition of samples which are intended to detect association between species and physical and other factors must be completely without bias in the sense that they should not be influenced by surface or vegetational features. Thirdly and perhaps most interestingly, the challenge is posed as to why vertical zonation should be reflected in biologically valid boundaries. Is it possible that quite different functional processes are occurring in different vertical strata and that we can thus localize distinct aspects of the decomposition process? This is one of the fields in which microbiologists are far ahead of soil zoologists. The work of the Liverpool school provides an emphatic affirmative answer to this question. Among soil zoologists very little work has yet been carried out in which samples have been related to clearly defined centres of activity or even to distinct vertical zones. Given sufficient effort such studies are certainly possible and could be most rewarding. There are however further difficulties. The vertical boundaries are not absolute; at any one time there is some intergradation of faunas and, perhaps more important, there is a good deal of evidence of vertical movement between horizons, at least in response to strong seasonal climatic change. STRENZKE (1952) has demonstrated this for oribatid mites in the cold North German winter. I investigated a series of three sites of different humidity in a Panamanian rain-forest in the dry season and although this is only a preliminary study I am satisfied that species which are limited to the true soil in the drier site penetrate much more freely into the litter in the damper site (*Table 1*). It seems probable that soil dwellers in the dry site would migrate up again into the litter in the wet season.

Studies of this kind, given sufficient understanding of soil structure and environmental factors, should provide material for association analysis of the kind which has been successfully performed by botanists working with large plants (GREIG-SMITH, 1964) which are localized on the soil surface. In the relatively simple 'soils' which were reconstituted after open-cast mining near Sutton Bonington and which lacked a complex vertical structure, DAVIS (1963) was able to carry through just such a study in order to detect characteristic complexes of species which were associated with particular conditions. However even if we can extend such studies into three dimensions I feel that we are to some extent confining our conceptual framework by working strictly in spatial terms.

TABLE 1

Analysis of percentage distribution in each of four vertical layers of the soil fauna from three sites on Barro Colorado Island, Panama
(sites 1, 2 and 3 chosen to represent a range from dry to moist; results based on about 1 m^2 made up of compounded subsamples)

	Site number 1				Site number 2				Site number 3			
Vertical layer	L	W	Sa	Sb	L	W	Sa	Sb	L	W	Sa	Sb
Malaconothrus sp.			53	47					4		96	
Uropodidae—A			100		25	75			3	4	90	4
—B			58	42	1	1	73	27			98	2
Trombididae adults			79	21	80	20			11		89	
Rhagidia sp.			94	6	1	3	72	24	23	8	60	
Entomobrya sp.	3		54	43	1		98		19	3	35	44
Protura			13	87	3	17	13	66		1	95	5
Japix sp.			32	68			76	24			59	41

L, leaf litter; W, woody litter; Sa, soil (upper 100 mm); Sb, soil (100–200 mm).

The 'species' are all those showing a difference in the ratio between the sites; all show a deeper distribution in the drier site and none show the reverse pattern of distribution.

Localization by Food Supply

The most significant ecological characteristics of any animals are, surely, that they move and that they have more or less limited feeding requirements. Micro-organisms lack the first attribute and exaggerate the second but the presence of animal transport may well render the difference less important than appears at first sight. It follows that we are more likely to understand biological affinities if we can elucidate the patterns of distribution which result from these two attributes.

With regard to mobility I shall say little. Ability to penetrate the progressively smaller passages with increased depth is a major discriminator of soil fauna as HAARLØV (1955) has shown. Generally speaking however, if the substrate is there and is not protected by major chemical barriers such as oxygen lack or pH changes, organisms will also be present to feed on it.

The amount of material contributed to the soil from the rest of an ecosystem is fairly closely circumscribed. In temperate conditions it is equivalent to about 1 kg of dry matter per m^2 (say 10,000 lb per acre), per annum. There is a normal range of two times above and below this figure in temperate conditions provided artificial enrichment has not taken place. In arctic or desert conditions, of course, the levels may be several times lower. To judge from published figures of litter-fall and gas-exchange rates, litter fall in tropical rain-forest is still only a few times above this level. (This rather surprising result is probably due to the high proportionate respiration of tropical plants and to some extent to proportionately more decomposition occurring before the plant material reaches the ground.)

This close constraint on the functional input to the soil food chains appears to be reflected in an equally narrow range of metabolic activity both of the soil fauna as a whole and also of the main constituent feeding types: carnivores, root-feeders, microbe-feeders etc., (MACFADYEN, 1963). These limitations on the range of major feeding types do not of course imply a corresponding restriction on the range of species involved. One of the outstanding things about soil biota is the immense range of species involved, many of them appearing to have similar feeding requirements. But it is also true that major segments of the biota appear to dominate in some soils and to become insignificant in others. For instance fly larvae of all kinds, but especially those of the Cyclorrhapha and the Tipulidae, can dominate in some soils, especially in woodlands. In many tropical soils the Diplura can outnumber all other insects and possess a dominant biomass, especially in the deeper layers. Ants and termites are other groups which can be extremely abundant in some but not all tropical soils.

Within these groups there can also be specialization which can help to account for the local occurrence of particular species. The succession of fungal species involved in the decomposition of litter (BURGES, 1955; WEBSTER, 1957) obviously provide an explanation of vertical localization within the profile and the specializations and restrictions of the fauna already referred to indicate good general reasons for zonation. There is also some evidence for quite specific feeding preferences in micro-arthropods; for example the demonstration (COLEMAN and MACFADYEN, 1966) that only certain species of arthropod were attracted to sterilized soil which had been reinoculated with particular fungi: the fungi involved were species which had been selected by the same animals in laboratory preference tests. Such studies will help us to piece together the nutritional requirements of individual species and to understand how they interact with each other. In the case of micro-organisms, however, it is clear that, since both substrate and product may often be extracellular and virtually indetectable, and since morphological identification is almost impossible in the field, quite new techniques are required. At present we look to highly localized biochemistry to provide information on the first and techniques such as the use of fluorescent antibody labelling and scanning electron microscopy for the second. This is, in reality, a problem of identifying function chemically whilst tracking down the originators of the functions on a microscopic scale.

CONCLUSION

The indications are that soil, despite its complexity, can be studied biologically and rationally. If we can detect the centres of activity, the sites of particular stages of decomposition processes, and link these to specific organisms, we should be able to isolate those centres of activity and processes which are important in particular soils and the organisms which are associated with them. The occurrence and magnitude of such 'industries' can then be used as a rational biological basis of the systematic study of soil.

ACKNOWLEDGMENTS

The adaptation of the figure by MOHR and VAN BAREN (1954) has been reproduced with the kind permission of Messrs W. van Hoeve, The Hague. The work on Barro Colorado Island was done whilst I was a guest of the Smithsonian Tropical Research Institute. I am indebted to the Institute for financial help and to the staff for every kind of practical assistance.

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